

GENERAL NOTES

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NOTES ON LARVAL MANDIBLE MORPHOLOGY OF *HYLEPHILA PHYLEUS PHYLEUS* (DRURY) (HESPERIIDAE, HESPERIINAE)

Additional key words: fiery skipper, grass-specializing feeders, scanning electron microscopy, caterpillars.

The present paper is part of a project describing the mandibular morphology of butterfly caterpillars and how it changes among larval instars. The goal is to recognize and better understand the behavior patterns within the four largest butterfly families in the Neotropics—Hesperiidae, Nymphalidae, Lycaenidae and Riodinidae (Heppner 1991, Brown 1996, Robbins & Opler 1997).

For butterflies, little is yet known about larval feeding strategies and how they evolved, especially in relation to mouthpart morphology and the characteristics of their foods. DeVries et al. (1985) examined variation in the mandibular morphology of some Nymphalidae caterpillars. With regard to the structure of the cutting edge, they recognized two morphological patterns—toothed vs. smooth mandibles. Smooth mandibles were coded as apomorphic, occurring in the subfamilies Satyrinae, Morphinae, Charaxinae, and Apaturinae. Recently, Ackery et al. (1999) suggested that the reduction and loss of larval mandibular teeth could be used to separate the grouping Heteropterae + Trapezitinae + Hesperinae from the other Hesperidae subfamilies.

For moths there is more information available. A number of species of the families Saturniidae, Sphingidae, Noctuidae and Notodontidae have been investigated (Bernays 1986, Bernays & Janzen 1988, Godfrey et al. 1989, Miller 1991, Dockter 1993, Dewhurst 1999, Passoa & Passoa 2000), and some patterns are hypothesized. Bernays & Janzen (1988), for example, showed two larval feeding strategies in Saturniidae and Sphingidae (snipping vs. chewing, respectively), considering these strategies as adaptive processes correlated with both the morphology of the mandibles as well as the physical and chemical features of the larval food plants. As in Nymphalidae (DeVries et al. 1985), smooth mandibles were found to be uncommon and an apomorphic feature in Notodontidae (as mentioned by Miller 1991). From the published information on the mandibular morphology of lepidopterous larvae, smooth mandibles seem to have had independent origins in the evolutionary history of Lepidoptera, as also occurred in Orthoptera (see Tables 2 and 3 in Bernays 1991).

The fiery skipper *Hylephila phyleus phyleus* (Drury, 1773) is a common species of open areas (Scott 1986).

It occurs from Canada to Rio Negro in southern Argentina, and throughout the Greater and Lesser Antilles (Evans 1955, Hayward 1973, Smith et al. 1994, MacNeill & Herrera 1999). The biology of the immature stages of *H. p. phyleus* has been described several times since it was recorded as one of the most serious lepidopterous pests of lawn grasses in Hawaii (Kawamura & Funasaki 1971, Tashiro & Mitchell 1985, Tashiro 1987, Toliver 1987). However, with regard to the immature morphology of this species, the descriptions are not very detailed.

The purpose of this paper is to describe the morphology of the mandibles and feeding habits of the five larval instars of *H. p. phyleus*. Ontogenetic changes in the mandibular morphology are documented with the aid of scanning electron microscopy (SEM). Mandibles of grass-feeding specialists (Isely 1944, Godfrey 1972, Brown & Dewhurst 1975, Bernays 1986) as well as of species feeding on other monocotyledonous plants (Peterson 1962, Casagrande 1979, DeVries et al. 1985, Ackery et al. 1999) have been characterized as having chisel-like edges (this is the terminology used by Bernays 1986; other names can be found elsewhere).

Specimens used in this study were obtained from eggs ($n = 26$) laid by a single female collected on 28 March 1999, at noon, in an urban lawn next to the railroad in the neighborhood of Cristo Rei, Curitiba, Paraná State, Brazil ($49^{\circ}16'15''\text{W}$ and $25^{\circ}25'48''\text{S}$, elevation 900 m). Before netting we observed oviposition behavior of *H. p. phyleus* for approximately 10 minutes. Our field observations corroborated the results of Tashiro & Mitchell (1985) who stated that "females [of a Hawaiian population of *H. phyleus*] alight on the turf for a few seconds for oviposition before flying a short distance to repeat the process". In the laboratory, the female was confined in a $30 \times 30 \times 30$ cm screen cage, fed 10% honey:water solution, and given fresh grass leaves daily for oviposition. After hatching, larvae were reared individually in plastic containers under greenhouse conditions with daylight temperatures that fluctuated from about 14 to 28°C and relative humidity of 63–88%. As larvae molted head capsules were preserved in 70% ethanol for future measurements and analyses. The mandibles were dissected following a specific methodology so that the other mouthparts and the head itself were not damaged (Godfrey 1987:551).

Left mandible width, here considered the lower edge of the mandible, and head capsule greatest width were measured with an ocular micrometer. These measurements are summarized in Table 1. Preparations for SEM analysis followed techniques in Bonatto & Carvalho (1996). Voucher specimens are deposited in the Coleção de Entomologia Padre Jesus Santiago Moure, Departamento de Zoologia, Universidade Federal do Paraná, Paraná, Brazil.

Few conspicuous changes in mandibular morphology were observed. Mandibles of all instars of *H. p. phyleus* are relatively short (ca. one-fourth of the head capsule greatest width, Table 1) with a broad base. This overall mandible shape is shared with other taxonomically unrelated lepidopterous species that eat either monocotyledons or dicotyledons with hard or tough leaves (Godfrey 1972, Brown & Dewhurst 1975, Casagrande 1979, Bernays & Janzen 1988, Bernays 1991). The cutting edge is flat and smooth with distinct notches that resemble inter-tooth depressions (Figs. 1–6). In worn mandibles these notches may be blurred or absent as a consequence of the abrasive agent (amorphous silica) deposited in the cell wall and cell lumen of grass leaves (Schoonhoven et al. 1998).

Mandibles of the first two larval instars of *H. p. phyleus* differ from the other instars by the number of setae and absence of a transverse ridge in the oral surface (Fig. 2, 3). Mandibular setae are present in all instars. In the first and second instars there are only two widely separated setae, with the one closer to the cutting edge slightly longer (Fig. 1, 3). Third instar larvae have three mandibular setae, with the longest seta about four times the length of the shortest (Fig. 4). In the last two instars the number and size of mandibular setae varies intraspecifically, but usually with two long setae and 4–6 short setae. In addition, the oral surface is deeply concave in the last two instars, and the transverse ridge is well developed (Figs. 5, 6) dividing the oral surface in two portions, the distal portion wider and shorter than the basal one where some pores (possibly glandular openings, see Snodgrass 1935:153–154) occur near the inner margin (Fig. 6).

The similarity of mandibular morphology among *H. p. phyleus* larval instars seems to be associated with the larval feeding strategy that is very similar in all instars (Fig. 7). Larvae of *H. p. phyleus* process the food plant by snipping off pieces of the plant tissue, which are swallowed after a quick mechanical processing by the oral surface of the mandibles. However, we predict that the leaf tissues are not mechanically processed by the first two larval instars due to the simplicity of the mandibular morphology, i.e., there is no transverse ridge nor any undulated area in the oral surface that

TABLE 1. Head capsule and left mandible widths (in mm) of fiery skipper larvae from Curitiba, Paraná State, Brazil. SD = standard deviation, N = number of specimens.

	Larval instars				
	1	2	3	4	5
Head capsule width					
Mean	0.48	0.68	1.00	1.57	2.24
SD	0.02	0.04	0.09	0.13	0.05
N	4	5	7	4	2
Left mandible width					
Mean	0.10	0.15	0.23	0.33	0.58
SD	0	0.02	0.03	0.03	0.01
N	4	5	7	4	2

may have a mashing or crushing function, as noticed in some notodontid species by Godfrey et al. (1989). Early instar larvae generally began consuming the edge of softer leaves. Third and subsequent instars readily accepted both young and old grasses. It is possible that younger larvae (first and second instars) of *H. p. phyleus* may have trouble in processing tougher grass leaves than mature larvae because of the high levels of silica and the arrangement of the lignified veins (Bernays 1986, 1991). The toughness or hardness in some grasses can be very high. For example, C4 grasses, i.e., species with a photosynthetic pathway producing a four-carbon acid, are about six times tougher than an average herbaceous plant (Bernays 1991).

Whether the presence of smooth mandibles in some lepidopterous larvae, at least during the late instars, is primarily associated with feeding on specific plant taxa, still awaits a thorough examination. DeVries et al. (1985:26) cited cases where the evidence does not support this hypothesis. A modified version of this hypothesis is that mandibular adaptations (toothed vs. smooth mandibles) of forb and grass feeders are associated with plant hardness or toughness (Bernays & Janzen 1988, Bernays 1991). Curiously, Ackery et al. (1999) have brought this topic for discussion again. While discussing on the monophyly of the grouping Heteropterinae + Trapezitinae + Hesperinae they suggested that 1) "a reduction and eventual loss of mandibular teeth" in Hesperidae could 2) "possibly be related to a diet of grasses and other tough monocotyledons" (in the original text of Ackery et al. sentences 1 and 2 are reversed). We hope that the present contribution stimulates other researchers to begin accumulating and reviewing as much information as possible on lepidopterous larval morphology, ecology and behavior.

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FIGS. 1-6. *Hylephila phlyeus phlyeus* (Drury). 1, anterior view of the head capsule of first instar larva, arrow indicating an inter-tooth like notch; 2, second larval instar, left oral surface; 3, idem, lower outer surface with two mandibular setae; 4, third larval instar, outer surface with three mandibular setae; 5, fifth larval instar, left mandible (oral view), arrow indicating transverse ridge; 6, idem, left mandible (oral view), arrow indicating "glandular" pores. Ba-mandibular base, La-labrum, Le-mandibular lower edge. Scale bar 100 μ m.

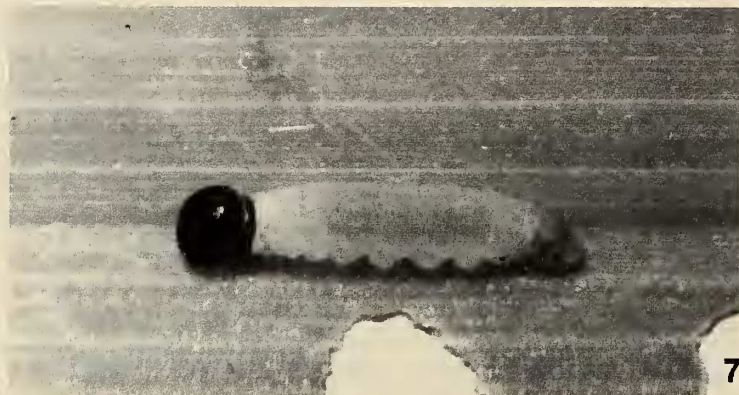


FIG. 7. *Hylephila phyleus phyleus* (Drury). First instar larva and characteristic damages in the leaf caused by snipping feeding behavior. Same behavior observed in the other larval instars.

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LITERATURE CITED

- ACKERY, P. R.; R. DE JONG & R. I. VANE-WRIGHT. 1999. The butterflies: Hedyloidea, Hesperioidea and Papilionoidea, pp. 263–300. In Kristensen, P. N. (ed.), Band/ Volume IV Arthropoda: Insecta. Lepidoptera, moths and butterflies: evolution, systematics, and biogeography. Vol. 1. In Fischer, M. (ed.), Handbuch der Zoologie. Handbook of Zoology. Walter de Gruyter, Berlin.
- BERNAYS, E. A. 1986. Diet-induced head allometry among foliage-chewing insects and its importance for graminivores. *Science* 231:495–497.
- . 1991. Evolution of insect morphology in relation to plants. *Phil. Trans. Roy. Soc. Lond. B* 333:257–264.
- BERNAYS, E. A. & D. H. JANZEN. 1988. Saturniid and sphingid caterpillars: two ways to eat leaves. *Ecology* 69(4):1153–1160.
- BONATTO, S. R. & C. J. B. DE CARVALHO. 1996. Análise morfológica das formas imaturas de *Sarconesia chlorogaster* (Wiedemann) (Diptera, Calliphoridae, Toxotarsinae). *Revta bras. Zool.* 13 (3):707–726.
- BROWN, E. S. & C. F. DEWHURST. 1975. The genus *Spodoptera* (Lepidoptera, Noctuidae) in Africa and the Near East. *Bull. Entomol. Res.* 65:221–262.
- BROWN JR., K. S. 1996. Diversity of Brazilian Lepidoptera: history of study, methods for measurement, and use as indicator for genetic, specific and system richness, pp. 221–253. In Bicudo, C. E. de M. & Menezes, N. A. (eds.), Biodiversity in Brazil: a first approach. CNPq–Conselho Nacional de Desenvolvimento Científico e Tecnológico, São Paulo.
- CASAGRANDE, M. M. 1979. Sobre *Caligo beltrao* (Illiger). I: Taxonomia, biologia, morfologia das fases imaturas e distribuições espacial e temporal (Lepidoptera, Satyridae, Brassolinae). *Rev. Bras. Biol.* 39 (1):173–193.
- DEVRIES, P. J., I. KITCHING & R. I. VANE-WRIGHT. 1985. The systematic position of *Antirrhoea* and *Caeois*, with comments on the classification of the Nymphalidae (Lepidoptera). *Syst. Entomol.* 10:11–32.
- DEWHURST, C. F. 1999. Changes in the morphology of the larval mandibles of African armyworm, *Spodoptera exempta* (Walker) (Lepidoptera: Noctuidae). *African Entomol.* 7 (2):261–264.
- DOCKTER, D. E. 1993. Developmental changes and wear of larval mandibles in *Heterocampa guttivitta* and *H. subrotata* (Notodontidae). *J. Lepid. Soc.* 47 (1):32–48.
- EVANS, W. H. 1955. A catalogue of the American Hesperidae indicating the classification and nomenclature adopted in the British Museum (Natural History). Part IV. Hesperidae and Megathyminae. British Museum (Natural History), London. 499 pp.
- GODFREY, G. L. 1972. A review and reclassification of larvae of the subfamily Hadeninae (Lepidoptera, Noctuidae) of America North of Mexico. U.S.D.A. Tech. Bull. 1450:1–265.
- . 1987. Noctuidae (Noctuoidea), pp. 549–578. In Stehr, F. W. (ed.), Immature insects. Vol. 1. Kendall/ Hunt Publishing Company, Dubuque, Iowa.
- GODFREY, G. L., J. S. MILLER & D. J. CARTER. 1989. Two mouthpart modifications in larval Notodontidae (Lepidoptera): their taxonomic distributions and putative functions. *J. New York Entomol. Soc.* 97 (4):455–470.
- HAYWARD, K. J. 1973. Catálogo de los ropalóceros argentinos. *Op. Lill.* 23:1–318.
- HEPPNER, J. B. 1991. Faunal regions and the diversity of Lepidoptera. *Trop. Lepid.* 2 (suppl. 1):1–85.
- ISELY, F. B. 1944. Correlation between mandibular morphology and food specificity in grasshoppers. *Ann. Entomol. Soc. Am.* 37:47–67.
- KAWAMURA, K. & G. FUNASAKI. 1971. [Note on] *Hylephila phylaeus*. *Proc. Hawaiian Entomol. Soc.* 21 (1):21–22.
- MACNEILL, C. D. & J. HERRERA G. 1999. Studies in the genus *Hylephila* Billberg, I. Introduction and the *ignorans* and *venusta* species groups (Hesperidae, Hesperinae). *J. Lepid. Soc.* 52 (3):277–317.
- MILLER, J. S. 1991. Cladistics and classification of the Notodontidae (Lepidoptera: Noctuoidea) based on larval and adult morphology. *Bull. Am. Mus. Nat. Hist.* 204:1–230.
- PASSOA, V. A. & S. PASSOA. 2000. Distribution and hostplant records for *Eupackardia calleta* from southeastern Texas with notes on mandibular morphology of Attacini (Saturniidae). *J. Lepid. Soc.* 53 (4):133–137.
- PETERSON, A. 1962. Larvae of insects: an introduction to Nearctic species. Part I. Lepidoptera and plant infesting Hymenoptera. Edited by the author, Columbus, Ohio. 315 pp.
- ROBBINS, R. K. & P. A. OPLER. 1997. Butterfly diversity and a preliminary comparison with bird and mammal diversity, pp. 69–82. In Reaka-Kudla, M. L., Wilson, D. E. & Wilson, E. O. (eds.), Biodiversity II: understanding and protecting our biological resources. Joseph Henry Press, Washington, D.C.
- SCHOONHOVEN, L. M., T. JERMY & J. J. A. VAN LOON. 1998. Insect-plant biology. From physiology to evolution. Chapman & Hall, London. 409 pp.
- SCOTT, J. A. 1986. The butterflies of North America: a natural history and field guide. Stanford University Press, California. 583 pp.
- SMITH, D. S., L. D. MILLER & J. Y. MILLER. 1994. The butterflies of the West Indies and South Florida. Oxford University Press Inc., New York. 264 pp.

- SNODGRASS, R. E. 1935. Principles of insect morphology. McGraw-Hill Book Company Inc., New York. 667 pp.
- TASHIRO, H. 1987. Turfgrass insects of the United States and Canada. Cornell University Press, Ithaca. 391 pp.
- TASHIRO, H. & W. C. MITCHELL. 1985. Biology of the fiery skipper, *Hylephila phyleus* (Lepidoptera: Hesperioidea), a turfgrass pest in Hawaii. Proc. Hawaiian Entomol. Soc. 25:131-138.
- TOLIVER, M. E. 1987. Hesperioidea (Hesperioidea), pp. 434-436. In Stehr, F. W. (ed.), Immature insects. Vol. 1. Kendall/Hunt Publishing Company, Dubuque, Iowa.

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NOTES ON THE HISTORIC RANGE AND NATURAL HISTORY OF *ANAEA TROGLODYTA FLORIDALIS* (NYMPHALIDAE)

Additional key words: *Croton*, Florida, West Indies, seasonal forms, parasitism.

Populations of the Florida leafwing, *Anaea troglodyta floridalis* F. (Comstock & Johnson) (Fig. 1), a butterfly endemic to south Florida and the lower Florida Keys, have become increasingly localized as its pine rockland habitat is lost or altered through anthropogenic activity (Baggett 1982, Hennessey & Habeck 1991, Schwarz et al. 1995, Salvato 1999, 2001). *Croton linearis* Jacq., (Euphorbiaceae) a subtropical species of Antillean origin, is the sole host plant for *A. t. floridalis* (Opler & Krizek 1984, Schwartz 1987, Minno & Emmel 1993, Smith et al. 1994). Once common throughout the pinelands of the lower Florida Keys (Dickson 1955), *C. linearis* now occurs only on Big Pine Key (Monroe Co.) and in fragmented populations on the southeast Florida mainland as far north as Jupiter Island (Martin Co.) (Salvato 1999). However, as host plant availability and appropriate habitat have declined, there is little recent evidence that *A. t. floridalis* ventures further north than southern Miami (Miami-Dade Co.) to make use of these fragmented host populations (Baggett 1982, Smith et al. 1994, Salvato 1999). Salvato (1999) has found few-documented field sighting records or museum collection specimens of *A. t. floridalis* from areas north of Monroe and Miami-Dade counties suggesting that this species may not have been common further north historically.

Delineating the precise historic range of *A. t. floridalis* has been further complicated by its confusion with Florida's other resident *Anaea* species, *Anaea andria* Scudder (Opler & Krizek 1984, Hennessey & Habeck 1991). An extremely tolerant species climatically, *A. andria* is widely distributed in the United States and Mexico (Pyle 1981, Opler & Krizek 1984). In Florida, Hernando County appears to represent the southern boundary for *A. andria* and this may correspond with the distribution of its host plants (Salvato

1999). *Anaea andria* uses several different *Croton* host species throughout its range, as opposed to *A. t. floridalis* which is stenophagic and will only use *Croton linearis* (Opler & Krizek 1984, Schwartz 1987, Hennessey & Habeck 1991, Smith et al. 1994, Worth et al. 1996). In northern Florida, *A. andria* primarily uses *Croton argyranthemus* Michx. (Glassberg et al. 2000) as a host, but will also feed on *C. capitatus* Michx (Opler & Krizek 1984, Salvato 1999). Salvato (1999), in preliminary feeding studies, found that when offered a variety of *Croton* species (*C. capitatus*, *C. linearis* and *C. argyranthemus*), *A. t. floridalis* larvae (n = 5) would only accept *C. linearis* as a food source. *Anaea andria* larvae (n = 5), when given the same selection, preferred *C. argyranthemus* as well as *C. capitatus* but refused to feed on *C. linearis*. The preference of *A. andria* for only northern occurring *Croton* species may explain why the butterfly has not established itself farther southward in the state. The apparently strict diet requirements of *A. t. floridalis* and possibly an inability to tolerate the colder winter climate of north Florida keep it from expanding northward. *Croton grandulosus* Michx. is the prevalent *Croton* species in the central part of Florida where neither butterfly occurs. Both *Anaea* species refused this plant as a host when offered it in feeding trials. Salvato is currently conducting continued feeding studies with *A. andria* and *A. t. floridalis* to establish larger sampling sizes. However, it does appear that an allopatric relationship occurs between *A. andria* and *A. t. floridalis* within Florida, one similar to that observed between other members of the genus within the West Indies (Smith et al. 1994). Figure 2 indicates the documented distribution of *A. t. floridalis* and *A. andria* in Florida.

Anaea t. floridalis maintains an appearance characteristic of the genus and the taxonomy of this sub-